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Social Wasps in Amber

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ABSTRACT

A new species of the paper wasp genus *Agelaia* Lepeletier (Hymenoptera: Vespidae; Polistinae, Epiponini) is described from Miocene amber of the Dominican Republic. *Agelaia electra* is the only social wasp known from Dominican amber.

Moreover, this species is the first Antillean representative of the tribe of paper wasps that founds new colonies exclusively by swarms, and thus shows that the tribe has become extinct in the Caribbean.

Few indeed are the social wasps known from the fossil record. A nest has been described from the Upper Cretaceous of Utah (Brown, 1941); its identity has been disputed (Bequaert and Carpenter, 1941), but recently it has been confirmed (Wenzel, 1990). However, the nest cannot be definitely assigned to either of the widespread subfamilies of social wasps, Vespinae or Polistinae. Cretaceous Vespidae are otherwise members of subfamilies with solitary behavior (Carpenter and Rasnitsyn, 1990; Brothers, 1992; Carpenter, unpubl.), and only a handful of putatively social species have been described from the Tertiary. Most of these latter fossils have been described as either *Vespa* or *Pol-*

istes (see lists in Carpenter, 1996, and Carpenter and Kojima, 1997). Bequaert (1930) discussed taxa that had been assigned to the Vespinae to that time, and concluded that most could be assigned at best to Vespidae. The sole exception was *Paleovespa baltica*, described by Cockerell (1910) from Baltic amber, which Bequaert determined to be possibly a vespine. Burnham (1978) reviewed the social wasp fossil record more recently, and concluded that no taxa prior to the upper Oligocene could definitely be assigned to Vespinae or Polistinae. Aside from several species of *Polistes*, the only other polistine genus listed was the epiponine *Polybia*. Two species of *Polybia* were described from Oli-

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gocene deposits in the Isle of Wight by Cockerell (1921a, 1921b). Both taxa were described from wings, and the first, *Polybia anglica*, was described as questionably a *Polybia* by Cockerell (1921a: 20), who stated that "This agrees in general with *Polybia*." Cockerell also compared the specimen to the epiponine *Apoica*, but his figure shows no particular resemblance to either genus—or to any polistine—in the radial region of the forewing as drawn. Cockerell (1921b) compared his *Polybia oblita* to *Polistes*, but again his figure resembles neither genus in particular, nor do the specific attributes mentioned characterize either genus. It is not possible to conclude with certainty that either fossil is even a polistine.

We report here the first fossil specimens that can be positively assigned to the polistine tribe Epiponini. This tribe is notable for the behavior of founding new colonies by swarms of queens and workers (Carpenter, 1993). Such behavior is derived in social wasps (Carpenter, 1989, 1991), having evolved once in the New World species and at least twice in the Old World (within the tribe Ropalidiini). The specimens before us are assignable to the genus *Agelaia* Lepeletier. *Agelaia* is a relatively basal genus in the Epiponini (Carpenter, 1991; Wenzel, 1993; Wenzel and Carpenter, 1994), with 23 extant species presently recognized (Richards, 1978; Silveira and Carpenter, 1996). The fossil specimens are an undescribed species.

Aside from being the oldest known specimens of this highly social lineage, these fossils from Dominican amber extend the range of the tribe Epiponini in space as well as time. The present distribution of Epiponini is Neotropical, ranging from Argentina to Mexico, with just a few species reaching as far as the U.S. border (Richards, 1978). In the Caribbean, aside from Trinidad, the tribe is almost totally absent, with just one species recorded from the Windward Islands (Grenada, Balthazar, and St. Vincent; Richards, 1978). Representatives of two other polistine tribes, the genera *Polistes* (Polistini) and *Mischocyttarus* (Mischocyttarini), are widespread in the Caribbean. These other two genera show the relatively primitive behavior of new colonies founded by one individual, which is sometimes joined by a few other

cofoundresses. The derived behavior of colony foundation by swarms is accomplished through chemical communication, by means of odor trails that guide the swarm to the new nesting location (see Jeanne, 1981). The presence of independent-founders and the absence of swarm-founders throughout the Caribbean has been explained as a limitation of the chemical trail system (Jeanne, 1981): swarms are unable to cross water barriers. This argument apparently does not explain the distribution of swarm-founding Ropalidiini in Southeast Asia, the Philippines, and Australia (although chemical communication has scarcely been studied in that tribe). The amber specimens show that the Epiponini once occurred in the Greater Antilles, and that their general absence from the West Indies at present is the result of extinction.

AGE OF THE AMBER

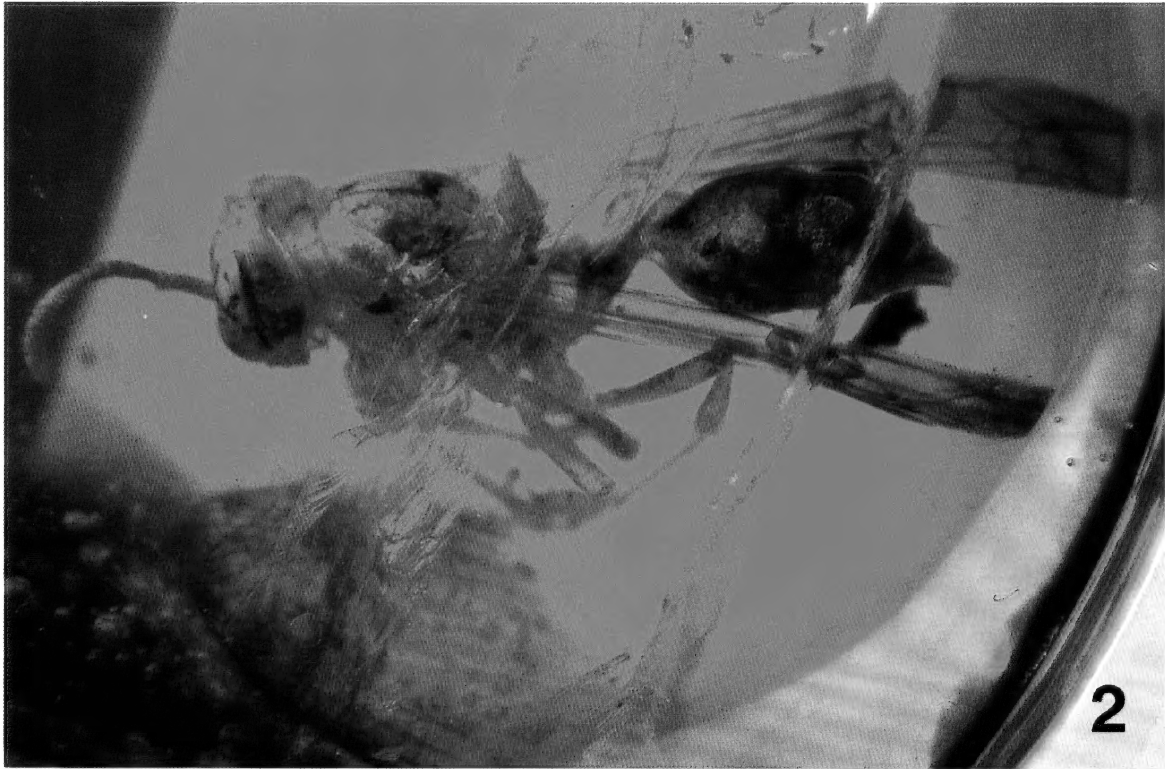
Although the specific provenance in the Dominican Republic of the three specimens studied here is unknown, the fossils are definitely Miocene in age. Grimaldi (1995) and Iturralde-Vinent and MacPhee (1996) assessed the published and new evidence regarding the stratigraphic position of Dominican amber deposits, and found the amber to date to mid to late-early Miocene (Iturralde-Vinent and MacPhee, 1996), at the earliest late Oligocene (Grimaldi, 1995). Previous claims (for example, Poinar, 1992) that Dominican amber is Eocene or even early Oligocene are erroneous.

Agelaia electra, new species

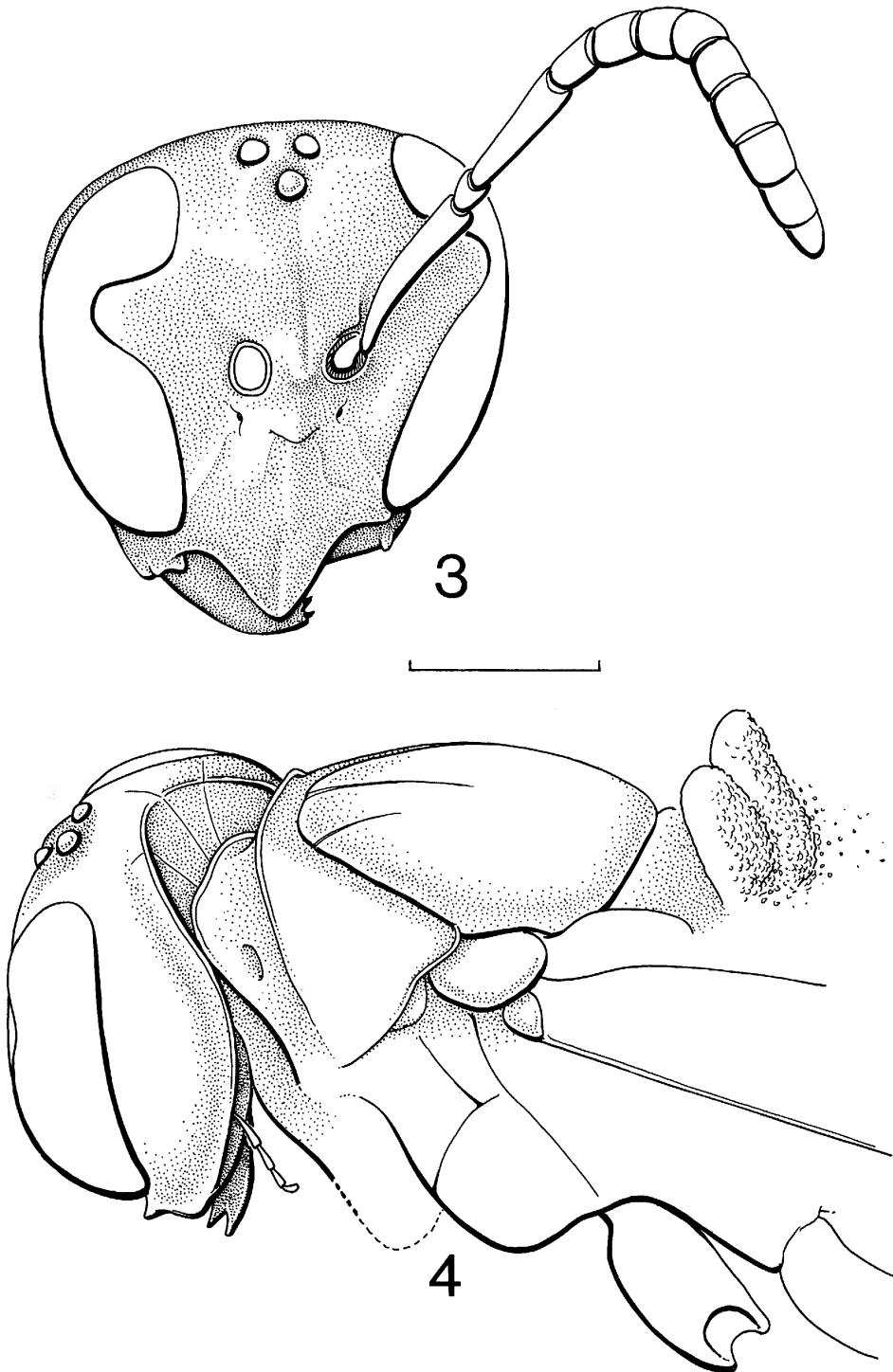
Figures 1–4

DIAGNOSIS: Recognizable as *Agelaia* by metasoma petiolate, mid- and hindtarsi with third and fourth tarsomeres symmetrical, pronotum with laterally straight dorsal carina and lateral fovea, scutum with posterolateral lamella adjoining tegula, ocelli separated from eyes by more than an ocellar diameter, occipital carina present, mesepisternum with oblique dorsal groove, metapostnotum carinate, and scutellum with median longitudinal furrow.

Distinguishable from extant species of *Agelaia* by almost uniformly pale color, with few maculations; eyes not hairy; forewing



Figs. 1–2. Habitus photographs of *Agelaia electra*, n. sp. 1. AMNH DR-SH-3: paratype. 2. AMNH DR-14-1040, holotype.



Figs. 3–4. Details of *Agelaia electra*, holotype. Scale bar = 1.0 mm. 3. Frontal view of face (slightly oblique). 4. Oblique lateral view of head and thorax.

length less than 10 mm, with prestigma longer than wide, tip rounded, costa without strongly projecting carina; tegula not produced anteriorly; pronotal dorsal carina not lobate, anterior carina low and not emarginate; first metasomal segment narrow, sides diverging from base to apex rather uniformly, with little angulation at spiracles.

DESCRIPTION: Female: (composite based on three specimens) forewing length 8.4–9.7 mm. Coloration largely brownish yellow, no obvious maculations. Vestiture inconspicuous, a few bristlelike hairs apparent on clypeus. Cuticle dull, sculpturing fine, impressed reticulation; clypeus about as broad as high, lateral margins little diverging and touching eyes for a distance greater than height of antennal socket, apex slightly produced, lateral lobes prominent; subantennal sulci evanescent; interantennal prominence low, with impressed median line; malar space shorter than height of antennal socket, without concave shining area; posterior ocelli separated by a distance about equal to their diameter; upper part of gena slightly narrower than eye in profile, widening below; occipital carina evanescent below; dorsal pronotal carina sharp but not high throughout its length, reaching laterally almost to level of fovea, then evanescent; fovea well developed, in small concavity; anterior pronotal carina not developed in front of fovea, frontal margin of pronotum with a moderately developed transparent lamella; lower part of pronotum not projecting; dorsal mesepisternal section with height twice its width; impressed line on scutellum distinct; propodeal furrow shallow, not well defined; first metasomal segment very narrow, width basally about one-tenth width of second segment, apically less than one-third width of second segment. **Male, Nest, Larva:** Unknown. It is possible that several small paper nests in Dominican amber, in private collections seen by D. Grimaldi, could belong to this species. None, unfortunately, were available for this study. Two of these nests are small and cup-shaped with a short peduncle; others were just some of the cells, with the rest of the nest lost at the surface of the amber. Living *Agelaia* usually construct paper nests in cavities, so these nests may not belong to this extinct species, but rather to a species of the genera *Polistes* or *Mischocyttarus*. Both

genera occur in the Dominican Republic at present, and build nests of pedunculate combs without envelopes.

TYPE MATERIAL: Holotype (AMNH-DR-14-1040) and one paratype (AMNH-DR-SH-3) in the American Museum of Natural History; one paratype in the British Museum (Natural History) (no. Pl II 320). The holotype was vacuum-embedded in synthetic casting resin because several fractures in the amber made preparation of the amber uncertain. Embedding allowed flat surfaces to be cut and polished close and parallel to the thorax, wings, and face. This particular specimen has two lobes that protrude upward from the posterior margin of the scutellum. They are not part of the wasp and appear to be a parasitic fungus. The AMNH paratype is in a small (2.5×1.5 cm) unprepared piece of amber, a photograph of which has been previously published (Grimaldi, 1996: 91). The BMNH paratype is embedded more deeply in an unprepared piece of amber. For esthetic reasons it was left intact, but this deep amber obscures some features of the wasp.

DISTRIBUTION: Miocene, Dominican amber.

ETYMOLOGY: The specific name refers to the finding of this species in amber.

REMARKS: Phylogenetic relationships among species of *Agelaia* have received little attention (Silveira and Carpenter, 1996). In the key of Richards (1978), *electra* keys to couplet 28, as can be seen by comparison of that key with the diagnosis given above. By the color characters given in couplet 28, *electra* keys out to *myrmecophila* (Ducke). It is not that species, which is complicated by the fact that *myrmecophila* sensu Richards is a mixture of species (Carpenter, 1997). True *myrmecophila* keys to *multipicta fulvanceps* in Richards' key; the taxon keyed as *myrmecophila* should evidently be known as *centralis* (Cameron). *Agelaia electra* is readily distinguished from *centralis* by the relatively narrower first metasomal segment, particularly basally. In *centralis*, the first segment has a basal width about one-fifth the width of the second segment, and an apical width much more than one-third the width of the second segment. The length of the first metasomal segment relative to the second segment is about the same in both species. The narrow first segment distinguishes *electra* from the

other species keying to that part of Richards' key, a group of species that might be called the *pallipes* group, although the monophyly of that group remains to be demonstrated. The shape of the first segment of *electra* is more like that found in species related to *angulata* but *electra* is much smaller than species of the *angulata* group, and it does not have the pronotal carina forming lateral lobes.

DISCUSSION: EXTINCTIONS

Grimaldi (1992a) discussed the biogeographic significance of a situation in which a fossil lies outside the distributional range of modern relatives. One cannot necessarily infer that a group was formerly more widespread just on the basis of a disjunct fossil. For example, we know that *Agelaia* occurred in what is now Hispaniola during the Miocene, but is not present there now; there is no fossil evidence documenting the presence of the genus anywhere in Central or South America during the Miocene (although this can be safely assumed). To make an inference of formerly more widespread distributions, it is essential to know the cladistic position of the fossil relative to modern species. If the disjunct fossil taxon is the most plesiomorphic member of a group of living species, as is the case of the North American Oligocene tsetse flies (Grimaldi, 1992a), one has extended the distribution of the group by addition of a plesiomorphic taxon—essentially done by broadening the definition of the group. Rigorous inference about formerly more widespread distributions can be made when a disjunct fossil has derived and primitive living relatives. For *Agelaia electra*, its relationships are with the *pallipes* group, all members of which are mainland Neotropical, as are other genera in the tribe. The inference can indeed be soundly

made that *Agelaia*'s distribution was widespread and once included what is now the Greater Antilles.

Agelaia is one of many other groups of Neotropical arthropods no longer occurring in the Caribbean. For social Hymenoptera other than the Vespidae, Caribbean extinctions preserved in Dominican amber are 12 genera of ants (Wilson, 1985) and the meliponine bees. *Proplebeia dominicana* is one of the most common species in Dominican amber, and several other, much rarer, undescribed meliponines exist in this amber (*Plebeia*, *Trigona*). Like epiponines, meliponine swarms are thought to have poor dispersal abilities across water barriers (Michener, 1979), and their modern absence from the Caribbean has been explained on this basis. Existence of an epiponine wasp, meliponine bees, and some Neotropical mainland ants in Dominican amber is not necessarily the result of continental drift of proto-Antillean land masses from nuclear America, as has often been conjectured (Poinar, 1992, 1996). As pointed out by Grimaldi (1992b), these fossils merely establish a possibility—they provide permissive evidence—that distributions were affected by drifting islands. Alternative and equally likely possibilities for distributions are extensive land bridges that connected many islands at various times, particularly in the Oligocene. Why these social insects, and perhaps others still undiscovered, became extinct is quite another problem for consideration.

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